Working the crowd: Sociable vervets benefit by reducing exposure to risk

ARTICLE *in* BEHAVIORAL ECOLOGY · JANUARY 2016

Tyler R. Bonnell
University of Lethbridge
15 PUBLICATIONS **83** CITATIONS
SEE PROFILE

Marcus Dostie
University of Lethbridge
3 PUBLICATIONS **8** CITATIONS
SEE PROFILE

Louise Barrett
University of Lethbridge
142 PUBLICATIONS **2,393** CITATIONS
SEE PROFILE

Peter Henzi
University of Lethbridge
126 PUBLICATIONS **4,175** CITATIONS
SEE PROFILE

Working the crowd: Sociable vervets benefit by reducing exposure to risk

Nathan Josephs[a,b], Tyler Bonnell[a,b], Marcus Dostie[a,b], Louise Barrett[a,b] and S. Peter Henzi[a,b]

[a]Department of Psychology, University of Lethbridge, 4401 University Drive, Lethbridge, Alberta T1K 3M4, Canada and [b]Applied Behavioural Ecology and Ecosystems Research Unit, University of South Africa, Private Bag X6, Florida, 1710 Republic of South Africa

Corresponding author: S.P. Henzi, Department of Psychology, University of Lethbridge, 4401 University Drive, Lethbridge T1K 3M4, AB, Canada. Email: peter.henzi@uleth.ca; Telephone: 1-403-3276835

Running head: Sociable vervets reduce exposure to risk

Keywords: ***Chlorocebus pygerythrus*****, dominance rank, grooming networks, vigilance, Voronoi tesselations, domains of danger**

INTRODUCTION

Primate sociality, as in many other animals, is driven by predation risk (van Schaik 1983; Majolo et al. 2008). Group-living does not, however, reduce risk equally across all group members. Indeed, long-standing theoretical considerations (Hamilton 1971), backed by empirical evidence (Ron et al. 1996; Quinn and Cresswell 2006; De Vos and O'Riain 2010), indicate that animals on the margins of groups are more vulnerable to attack because they have larger 'domains of danger'.

Predation-driven sociality also entails unavoidable competition for local resources (van Schaik 1983; Dunbar 1988), generating a potential trade-off between the need to forage efficiently (generally achieved by keeping at a distance from others) and maintaining a safe position within the group (achieved by keeping in close proximity to others). This means that an animal should position itself relative to other group members in ways that maximise the benefits from reduced risk while minimising the costs of scramble competition (Krause and Ruxton 2002; Morrell and Romey 2008). This task will be easiest for animals that, directly or indirectly, regulate the movement and location of others. Not surprisingly, therefore, most accounts identify physical size and/or social rank (Hirsch 2010) as the primary individual attributes driving the spatial structure of groups. In the main, higher ranking animals in monkey groups occupy the centre, where their rank still affords them priority of access to resources, while subordinates occupy the margins, where increased predation risk may carry some compensation in the form of improved foraging opportunities (Robinson 1981; Collins 1984; Janson 1990; Hall and Fedigan 1997; Heesen et al. 2014).

Given the strength of selection imposed by predation, however, we would expect disadvantaged group members to attempt to attenuate or circumvent the strictures imposed by rank. As the extent of exposure to risk is set by the proximity of others, one obvious route to safety runs through the use or exploitation of grooming to cultivate social ties that reduce exposure. Data from groups or species in which there is a preference for grooming up the dominance hierarchy, provide implicit evidence for this. While this is usually explained in terms of coalitionary support (Seyfarth 1980; Schino 2006), it also holds that if dominant animals are less exposed to risk, this must also be true for the groomer; more so if the spatial association persists beyond the grooming bout. This allows us to distinguish between the benefits of providing grooming ('social effort') and the passive benefits that accrue to being a target of grooming ('popularity'). Unfortunately, grooming partners in such systems are usually closely ranked, making it difficult to determine whether lower-ranking animals are motivated to groom dominant animals but are competitively excluded, or whether they simply avoid clusters of high ranking females (Henzi and Barrett 2007), the latter of which then groom one another because they are spatially associated.

We work on a population of vervet monkeys (*Chlorocebus pygerythrus*) that is characterised by large mean group size and high predation (Pasternak et al. 2013; Van de Ven et al. 2013; Ducheminsky et al. 2014). In these groups, the presence of strong, linear dominance hierarchies does not underpin social preference, neither prior to (Henzi et al. 2013; Matlock 2013) nor at the time of the current study (Josephs 2015) and it is likely that the size and dispersion of our groups attenuates the influence of rank as a structuring force (Henzi and Barrett 2007) and instead promotes the benefits of broad social integration (McFarland et al. 2015).

Here, we use spatially explicit data to test the prediction (i) that group members who give and receive more grooming, but not those that are high ranking, have smaller domains of danger and spend less time vigilant, which is the proximate index for predation risk (Robinson 1981). We also consider the possibility that safety seeking involves a trade-off against foraging efficiency (Krause 1994; Bumann et al. 1997). If animals tolerate larger domains of danger in order to eat without impediment, we expect (ii) to see this reflected as an increase in foraging time, which is our measure of efficiency. Recent evidence suggests that high-ranking vervets make this trade-off by leading the group (Teichroeb et al. 2015. See also Janson 1990 for capuchin monkeys). As a subsidiary prediction, therefore, we test whether (iii) if not central, dominant animals are more likely to be found at the front of the troop.

To assess the first two predictions, we make use of bounded Voronoi tesselation (James et al. 2004) as a way to develop a more animal-centered measure of predation risk. In most studies, the centre of mass of the troop is calculated, and animals' positions are assessed relative to this centre. This imposes a human viewpoint on spatial distribution, and makes the implicit assumption that animals have some sense of the centre of the troop and position themselves accordingly. As this seems inherently unlikely to be the case, we make the more realistic assumption that animals monitor the presence of others in their field of view and adjust their position accordingly. Voronois tesselation better captures this process and allows the calculation of domains of danger in terms that are more likely to reflect the animals' perceptual experience.

METHODS

Study animals and site

Data were collected between January 2014 and May 2014 from two habituated troops of vervet monkeys (N_{PT}= 25; N_{RBM}=43), occupying a predator-rich, semi-arid riparian woodland in in South Africa (Pasternak et al. 2013). All subjects were identifiable from natural markings and could be approached on foot to within 1m. Observational data collection protocols were approved by the University of Lethbridge Animal Welfare Committee (Protocol 0702).

Spatial data collection

Individual spatial locations were recorded with handheld, GPS-enabled computers (Trimble Nomad). While the absolute recording error was ~5m, the relative error of inter-individual distances was ~1m. To construct realistic domains of danger, we collected time-stamped GPS records for all non-infant troop members (N_{PT}=17; N_{RBM}=34) at one of two pre-determined times (~0800h and ~1600h) on each field day (hereafter called "sweeps"). Three to four data collectors for RBM, and one to three for PT, collected data on the identity and location of as many individuals as possible over a 10min period. Positions were recorded by standing next to the animals or, if they were arboreal, by standing at the base of the tree. To maximise encounter rate, we did not record activity during these sweeps. As each observer collected points independently, we acquired repeated point locations for most subjects. We completed a total of 147 sweeps (N_{RBM}=73; N_{PT}=74). The mean number of individuals identified per sweep was 14.4±1.9 SD for PT and 25.6±4.0SD for RBM. We found no systematic variation in our ability to detect individuals and exclusion from a sweep was likely to have been a consequence of the animal's location at the centre of one of the very dense thickets that typify the study site.

GPS data were entered into ArcGIS 10.2 (ESRI 2011). To generate a snapshot of the individual positions at a single moment, we used interpolation and group movement extrapolation. We first identified the time during the sweep that maximised the number of subjects for which we had data both earlier and later. We then interpolated their position to that time, using the standard assumption of movement in a straight line at a constant speed, which, for the time between successive records in our data, has a small margin of error (Dostie 2014). To infer the position of subjects without repeated data, we determined the mean movement velocity of subjects for which we had more than one point location. Depending on whether the positions had been collected before or after the designated snapshot time, we then assigned locations either by adding or subtracting this mean movement velocity from the recorded positions (see Josephs 2015 for detail).

We used the area (m^2) of Voronoi tesselations as an index of the extent of an animal's exposure to risk (Hamilton 1971). To set the limits of marginal tesselations (James et al. 2004), we used the modal distance (15m) at which our animals first indicated that they had seen both natural and model land and aerial predators (N. Ducheminsky, unpublished data). The direction of travel of the troop was determined from the average direction of travel of resampled individuals and was used to identify the animal at the front of the troop. The straight-line distance of each subject to a line drawn through the front animal, perpendicular to the direction of travel, was recorded as its distance from the front. A sample snapshot illustrating interpolated domains of danger and location in relation to the direction of travel is provided in Figure 1.

Activity and social networks

We used instantaneous scan samples (J. Altmann 1974), taken every 30 minutes, to record the activity of visible subjects (N_{PT}=7584 records, N_{RBM}=9446 records) over the study period. We identified four behavioural states (foraging, moving, resting and grooming) as well as vigilance, recorded when an animal was visually scanning the environment beyond its immediate surroundings (Baldellou and Henzi 1992). These data allowed us to estimate the proportion of time spent in each of these states by each subject over the study period. A subset, comprising those scans taken just prior to each sweep, was used to establish general activity schedules at the time of the sweep. When animals were allogrooming, we identified both partners and noted their roles (groomer/recipient). We used these to generate weighted, directed grooming interaction matrixes for each troop, with the value for each member of a dyad (A,B), calculated as:

$N_G/(N_A+N_B)$,

where, depending on the matrix, N_G is either the frequency of A's grooming given to - or received from - B, while (N_A+N_B) is the sum of the total number of scans recorded for A and B.

To quantify social effort and popularity respectively, we used UCINET 6 software (Borgatti et al. 2002) to generate estimates, for grooming received and given respectively, of In-and Out-Strength Centrality for each subject. Strength estimates the weight of an individual's association with its direct associates. Centrality reflects the extent to which individual nodes in a network are connected to others. It is computed as the sum of the weights of the edges (weighted grooming interactions) that connect the node (subject) to other nodes (Whitehead 2008).

To conform to other current analyses by our group (Murphy et al. in prep.) we used In- and Out-Strength Centrality as the measure of association breadth, rather than the number of partners (McFarland et al. 2015), after confirming that the two estimates were strongly positively correlated (Tables S1 and S2). The significant negative correlations between In- and Out Strength Centrality and network measures of variation in grooming diversity (In- and Out CV. Table S2) also established that our measures could differentiate between broad and restricted social engagement. At the same time, In- and Out-Strength Centrality were not themselves correlated. We are confident, therefore, that these single measures of sociability are able to capture the nature of social engagement identified in the predictions, with each independently providing a measure of the extent of an animal's sociability.

We restricted final analyses to those animals that were integrated into the adult social dominance hierchardy (N_{PT}=14; N_{RBM}=28).

Dominance

Data from ongoing, ad libitum observations across the study period allowed us to construct separate dominance hierarchies for each sex in each troop based on the outcome of all observed, decided agonistic events. Each animal's rank was expressed as a normalized David's score (Stevens et al. 2005), which was then standardised to facilitate comparisons across sex and troop (Henzi et al. 2013).

Statistical analysis

We entered standardised dominance rank, grooming in-strength centrality and grooming out-strength centrality as fixed effects in each of two linear mixed models to assess the effects of sociability and dominance on (i) the extent of exposure and (ii) the probability of being in the vanguard of the troop. Troop identity and subject sex were entered as control variables. Subject identity was entered as a random effect. Following Barr et al. (2013), we specified random slopes for as many predictor variables as still allowed the model to converge.

In the absence of data of adequate resolution at the level of the sweep, we used single linear models to regress (a) mean exposure and (b) mean distance from the front of the group on foraging and vigilance aggregated across the study period. Mean exposure and mean distance from the front for each adult across the study period were entered as the criterion variables and the proportions of time that it spent foraging and vigilant as predictor variables, after determining that foraging and vigilance were not correlated (r=-0.127, N=42, P=0.42. Data are provided in Table S1). We entered Troop and Sex as control variables.

As we had no a priori predictions for interactions, we ran each model with main effects and then, after testing whether they differed significantly from the control models, using the Akaike information criterion (AIC) and likelihood ratio tests to do so, we did the same to determine whether the models were improved by the addition of interaction terms. We evaluated the distributions of the criterion variables and the residuals of final models, and compared obtained standard errors to robust standard errors (King and Roberts 2015). The models we report are those that best met the assumptions of normal error structure and were run using STATA 14 statistical software (StataCorp 2015). We used Cohen's f^2 as a measure of relative effect size (Selya et al. 2012). Alpha was set at 0.05.

RESULTS

Social influences on exposure

We ran the model with random slopes on both in- and out-strength centrality. While the main-effects model differed from the control model (ΔAIC: -10.12, $X^2_3 = 16.12$, P=0.001), the two-way interaction model made no additional contribution (ΔAIC: 4.69, $X^2_3 = 1.31$, P = 0.727). The whole model was significant (Log likelihood = -15702.103; Wald $X^2_5 = 40.51$; P = 0.0001) and differed from the equivalent linear model without random effects ($X^2_3 = 15.48$, P = 0.017). Parameter estimates for fixed effects (Table 1) indicate significant negative relationships between degree of Exposure and both Grooming out-strength ($f^2 = 0.033$) and Grooming in-strength centrality ($f^2 = 0.011$. Figure 2), as well as for Troop Identity. Examination of the pattern of ongoing activity indicates that these results were not a consequence of conducting the sweeps when the modal activity was grooming (Figure 3). While the overall distribution differed from expectation ($X^2_3 = 347.37$, P = 0.000), only grooming had an observed value that was lower than expected. Individual estimates of mean exposure are illustrated in Figure S1.

--Table 1--
--Figure 2--
--Figure 3--

Social influences on distance from the front

We standardised distance from the front of the troop by expressing it as a proportion of the distance between the front and back animals. We then ran the model with dominance and the social network measures as fixed effects, together with a random slope on out-strength centrality. We found no support for the prediction that dominant animals were closer to the front of the group (Table 1). The model was not significant (Wald $X^2_5 = 6.68$, P=0.245) and differed from neither the control (ΔAIC: 4.16, $X^2_3 = 2.7$, P = 0.441), nor the null model (ΔAIC: 2.16, $X^2_5 = 7.83$, P=0.166). Individual estimates of mean exposure by rank are provided in Figure S2.

The effect of mean exposure on foraging and vigilance

The results of the regression are reported in Table 2a. While the main-effects model was significant ($F_{4,37} = 6.084$, P = 0.0007. Adj. $R^2 = 0.33$) and differed from the control model (ΔAIC: -6.28, $X^2_2 = 10.27$, P = 0.006), the interaction model made no additional contribution (ΔAIC: +1.92, $X^2_1 = 0.07$, P = 0.79). Parameter estimates indicate that while vigilance increased significantly with increasing exposure ($f^2 = 0.151$), foraging effort decreased ($f^2 = 0.116$). These outcomes are illustrated in Figure 4.

--Table 2--
--Figure 3--

--Figure 4--

The effect of mean distance from the front on foraging and vigilance

The results of the regression are reported in Table 2b. The main-effects model was not significant ($F_{4,37} = 1.67$, P = 0.177. Adj. $R^2 = 0.06$). Parameter estimates confirm the difference between the sexes but reveal no significant effects for either vigilance ($f^2 = 0.0001$) or foraging effort ($f^2 = 0.002$).

DISCUSSION

Our results support the prediction that increased social integration carries a beneficial reduction in exposure to risk in adult vervet monkeys. More particularly, animals that are sociable - i.e. invest in grooming a wide array of partners, or who are extensively groomed by others - have smaller domains of danger and, even if only in the aggregate (Pollet et al. 2015), spend less time vigilant and more time foraging. These twin benefits indicate that there has been no simple trade-off between safety and dominance-controlled access to resources for lower-ranking animals (Krause 1994). This may well stem from the fact that the spread of large groups in a mosaic habitat makes it easier, on the whole, to avoid agonistic contact (Hemelrijk 2000; Henzi and Barrett 2007). There is support for this in the earlier finding that, while the rate of food-related aggression in our large groups does not differ from that recorded in smaller groups, the overall rate of aggression is much lower (Henzi et al. 2013). That is, while animals may clash at concentrated food sources, they are less likely to do so under other circumstances. In the absence of the structuring influence of dominance rank, therefore, lower exposure to predation risk appears to be an unalloyed good for those that can engineer it.

Our relatively large, dispersed groups may also explain why higher ranking animals were not more likely to be found at the front of their groups. In these diffuse groups, as our results indicate, the 'front' may be an inadequate index of foraging potential and predation risk. That is, animals do not forage in a way (i.e., in some form of 'file' formation) that would result in there being a leading edge of animals that encounters new foraging patches ahead of all other animals, and would present a foraging advantage. Rather, in the case of such diffuse groups, a measure such as access to unimpeded foraging swathes, as suggested by Altmann (S.A. Altmann 1974), is probably more appropriate, i.e., where animals attempt merely to forage along a trajectory that reduces the likelihood that they will encounter other animals in their path. The domains of danger we used in this study are likely to be a better index of risk from the animal's perspective.

Methodologically, our results point to the utility of using spatially explicit information in the analysis of social dynamics (Henzi and Barrett 2007). Until recently, for example, the use of qualitative or abstracted estimates of position to identify individuals at the 'edges' and 'centres' of groups, has necessarily reflected procedural constraints that then impose a human-centred analytical framework that may only incidentally capture what is relevant to the animal itself (see Isbell et al. 1998). As things stand, it is unclear whether our results differ from those observed elsewhere (Teichroeb et al. 2015) or other species (Heesen et al. 2014) because of differences in approach or whether they reflect the structuring effects of local environments and group size. Regardless of the outcome, converging on a common, realisable methodology will make it possible to interrogate such questions in productive and interesting ways.

Admittedly, the effect sizes in our study are small. This no doubt reflects the fact that our analysis is rather coarse-grained and that we have not characterised the environment fully in terms of variation in risk. That is, there are areas where actual predator densities are higher, and areas where risk of predation is higher due to the specifics of habitat structure. It may also be the case that movements near territory boundaries and the increased likelihood of inter-group encounters have an effect on spatial positioning within the troop that differs from the response to predation risk. All of these factors are likely to account for some of the unexplained variance, and we are currently working on further analyses to assess the impact of such effects. At the same time, our positional data are relatively coarse-grained, which results in somewhat noisy analyses although this is both demonstrably and powerfully remediable (Strandburg-Peshkin et al. 2015), even if not always practical. Given its economy and relative ease of implementation, our aim here has been to demonstrate the overall utility of such an approach to studies of spatial structure, and, while even low-resolution data can be made to reveal underlying decision-rules during movement (Bonnell et al. 2015), it is clear that more fine-grained analyses will only help improve our understanding of how this is emerges in real-time.

The absence of rank-dominated social structure also reveals three things of relevance to the current concern with social influences on fitness outcomes (Silk et al. 2003; Berghänel et al. 2010). First, it provides evidence that the short-term benefits of smaller domains of danger are not the passive consequence of patterns of spatial segregation mediated by rank or kinship (Henzi and Barrett 2007), but can actively be pursued by group members, with the effects persisting beyond the interaction itself. Here, given that an animal's popularity is necessarily determined by the extent to which others groom it, its advantages are a by-product of others' social effort, and consequently less effective. On the whole, then, it appears better for vervets to give than to receive.

Second, regardless of grooming direction, the benefits of spatial position accrue to those in both sexes with broad, rather than narrow, social ties. While much attention has been directed at the advantages of strong ties to a few associates (Silk et al. 2009), our results, both here and elsewhere (McFarland et al. 2015. See also Murphy et al. in prep. for baboons), suggest that there are good reasons for social animals also to sustain wider affiliations. Also, while most studies have emphasised the long-term fitness benefits of sociability (Silk et al. 2009; Archie et al. 2014), our results, both here and elsewhere (McFarland et al. 2015), are beginning to identify the more immediate mechanisms by which patterns of social interaction come to generate fitness outcomes.

Third, and finally, assessing whether the tension between strong, ultimately competitive bonds, where different clusters of closely associated animals within a group vie for advantage (Cheney et al. 2012), and weak, integrative ties is constant and inherent, or whether the relative value of each differs across time and/or populations and taxa, represent fruitful lines of enquiry, not only in terms of individual strategies but also with respect to the stability of groups. With respect to the latter, the dominant argument has been that group fission follows inevitably from the increased within-group competition associated with increasing troop size, with cleavage following time constraints on the ability of individuals to sustain strategic alliances (see, for example, Dunbar 1997). Our observation of the attenuation of rank effects, alongside evidence of the benefits of broad social integration suggests that the dynamics of group fission may be more interestingly nuanced than generally presented, at least in these larger vervet groups.

ACKNOWLEDGEMENTS

We thank two anonymous referees for their constructive input. Mark and Sarah Tompkins kindly allow us to work at Samara and Kitty and Richard Viljoen provide constant support for the project in a number of ways. We are grateful to Nicola Guthrie, Marta Ricart Fincias, and Jonathan Jarrett for their generous help with data collection. The study was funded by NSERC (Canada) Discovery grants to SPH and LB and NRF (South Africa) Incentive funding to SPH. TB is supported by an FRQNT Fellowship and funds from LB's Canada Research Chair award.

REFERENCES

Altmann J. 1974. Observational sampling of behavior: sampling methods. Behaviour. 49:227–266.

Altmann SA. 1974. Baboons, space, time, and energy. Am Zool. 14:221–248.

Archie EA, Tung J, Clark M, Altmann J, Alberts SC. 2014. Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. Proc R Soc Biol Sci Ser B. 281:20141261.

Baldellou M, Henzi SP. 1992. Vigilance, predator detection and the presence of supernumerary males in vervet monkey troops. Anim Behav. 43:451–461.

Barr DJ, Levy R, Scheepers C, Tily HJ. 2013. Random effects structure for confirmatory hypothesis testing: Keep it maximal. J Mem Lang. 68:255–278.

Berghänel A, Ostner J, Schröder U, Schülke O. 2010. Social bonds predict future cooperation in male Barbary macaques, *Macaca sylvanus*. Anim Behav. 80:675–682.

Bonnell TR, Henzi SP, Barrett L. 2015. Sparse movement data can reveal social influences on individual travel decisions. ArcXiv 1511.01536.

Borgatti SP, Everett MG, Freeman LC. 2002. Ucinet for Windows: Software for social network analysis. Analytic Technologies.

Bumann D, Krause J, Rubenstein D. 1997. Mortality risk of spatial positions in animal groups: the danger of being in the front. Behaviour 134:1063–1076.

Cheney DL, Silk JB, Seyfarth RM. 2012. Evidence for intrasexual selection in wild female baboons. Anim Behav. 84:21–27.

Collins DA. 1984. Spatial pattern in a troop of yellow baboons (*Papio cynocephalus*) in Tanzania. Anim Behav. 32:536–553.

De Vos A, O'Riain MJ. 2010. Sharks shape the geometry of a selfish seal herd: experimental evidence from seal decoys. Biol Let. 6:48–50.

Dostie MJ. 2014. Determining the optimal revisit time for primate spatial data collection. MSc Dissertation, University of Lethbridge.

Ducheminsky N, Henzi SP, Barrett L. 2014. Responses of vervet monkeys in large troops to terrestrial and aerial predator alarm calls. Behav Ecol. 25:1474–1484.

Dunbar RIM. 1997. Determinants of group size: a general model. In: Runciman WG, Maynard-Smith J, Dunbar RIM, editors. Evolution of social behaviour patterns in primates and man. Oxford: Oxford University Press. p. 33-58.

Dunbar RIM. 1988. Primate Social Systems. London: Chapman and Hall.

ESRI. 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

Hall CL, Fedigan LM. 1997. Spatial benefits afforded by high rank in white-faced capuchins. Anim Behav. 53:1069–1082.

Hamilton WD. 1971. Geometry for the selfish herd. J Theor Biol. 31:295–311.

Heesen M, Macdonald S, Ostner J, Schülke O. 2014. Ecological and social determinants of group cohesiveness and within-group spatial position in wild Assamese macaques. Ethology 121:270–283.

Hemelrijk CK. 2000. Towards the integration of social dominance and spatial structure. Anim Behav. 59:1035–1048.

Henzi SP, Forshaw N, Boner R, Barrett L, Lusseau D. 2013. Scalar social dynamics in female vervet monkey cohorts. Philos Trans R Soc Lond B Biol Sci. 368:20120351.

Henzi SP, Barrett L. 2007. Coexistence in female‐bonded primate groups. Adv Study Behav. 37:43–81.

Hirsch BT. 2010. Within-group spatial position in ring-tailed coatis: balancing predation, feeding competition, and social competition. Behav Ecol Sociobiol. 65:391–399.

Isbell LA, Pruetz JD, Young TP. 1998. Movements of vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) as estimators of food resource size, density, and distribution. Behav Ecol Sociobiol. 42:123–133.

James R, Bennett PG, Krause J. 2004. Geometry for mutualistic and selfish herds: the limited domain of danger. J Theor Biol. 228:107–113.

Janson CH. 1990. Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. Anim Behav. 40:922–934.

Josephs N. 2015. Social and Spatial Structure in Vervet Monkey Troops. MSc Dissertation. University of Lethbridge.

King G, Roberts ME. 2015. How robust standard errors expose methodological problems they do not fix, and what to do about it. Political Analysis 23:159–179.

Krause J. 1994. Differential fitness returns in relation to spatial position in groups. Biol. Rev (Camb). 69:187–206.

Krause J, Ruxton GD. 2002. Living In Groups. Oxford: Oxford University Press.

Majolo B, de Bortoli Vizioli A, Schino G. 2008. Costs and benefits of group living in primates: group size effects on behaviour and demography. Anim Behav. 76:1235–1247.

Matlock A. 2013. Negotiating Social Space in Vervet Monkeys. MSc Dissertation. University of Lethbridge

McFarland R, Fuller A, Hetem RS, Mitchell D, Maloney SK, Henzi SP, Barrett L. 2015. Social integration confers thermal benefits in a gregarious primate. J Anim Ecol. 84:871–878.

Morrell LJ, Romey WL. 2008. Optimal individual positions within animal groups. Behav Ecol. 19:909–919.

Pasternak GM, Brown LR, Kienzle S, Fuller A, Barrett L, Henzi SP. 2013. Population ecology of vervet monkeys in a high latitude, semi-arid riparian woodland. Koedoe 55:Art. #1078.

Pollet TV, Stulp G, Henzi SP, Barrett L. 2015. Taking the aggravation out of data aggregation: A conceptual guide to dealing with statistical issues related to the pooling of individual-level observational data . Am J Primatol. 77:727-740.

Quinn JL, Cresswell W. 2006. Testing domains of danger in the selfish herd: sparrowhawks target widely spaced redshanks in flocks. Proc R Soc Biol Sci Ser B. 273:2521–2526.

Robinson JG. 1981. Spatial structure in foraging groups of wedge-capped capuchin monkeys *Cebus nigrivittatus*. Anim Behav. 29:1036–1056.

Ron T, Henzi SP, Motro U. 1996. Do female chacma baboons compete for a safe spatial position in a southern woodland habitat? Behaviour. 475–490.

Schino G. 2006. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. Behav Ecol. 18:115–120.

Selya AS, Rose JS, Dierker LC, Hedeker D, Mermelstein RJ. 2012. A practical guide to calculating Cohen's f2, a measure of local effect size, from PROC MIXED. Front Psychol. 3

Seyfarth RM. 1980. The distribution of grooming and related behaviours among adult female vervet monkeys. Anim Behav. 28:798–813.

Silk JB, Beehner JC, Bergman TJ. 2009. The benefits of social capital: close social bonds among female baboons enhance offspring survival. Proc R Soc Biol Sci Ser B. 276:3099–3104.

Silk JB, Alberts SC, Altmann J. 2003. Social bonds of female baboons enhance infant survival. Science. 302:1231–1234.

StataCorp. 2015. Stata Statistical Software: Release 14. StataCorp, College Station, TX. StataCorp, College Station, TX.

Stevens JMG, Vervaecke H, de Vries H, Van Elsacker L. 2005. The influence of the steepness of dominance hierarchies on reciprocity and interchange in captive groups of bonobos (*Pan paniscus*). Behaviour 142:941–960.

Strandburg-Peshkin A, Farine DR, Couzin ID, Crofoot MC. 2015. Shared decision-making drives collective movement in wild baboons. Science 348:1358–1361.

Teichroeb JA, White MMJ, Chapman CA. 2015. Vervet (*Chlorocebus pygerythrus*) intragroup spatial positioning: Dominants trade-off predation risk for increased food acquisition. Int J Primatol. 1–23.

Van de Ven TMFN, Tambling CJ, Kerley GIH. 2013. Seasonal diet of black-backed jackal in the eastern Karoo, South Africa. J Arid Environ. 99:23–27.

van Schaik CP. 1983. Why are diurnal primates living in groups. Behaviour. 87:120–144.

Whitehead H. 2008. Analyzing animal societies: quantitative methods for vertebrate social analysis. University of Chicago Press.

Figures

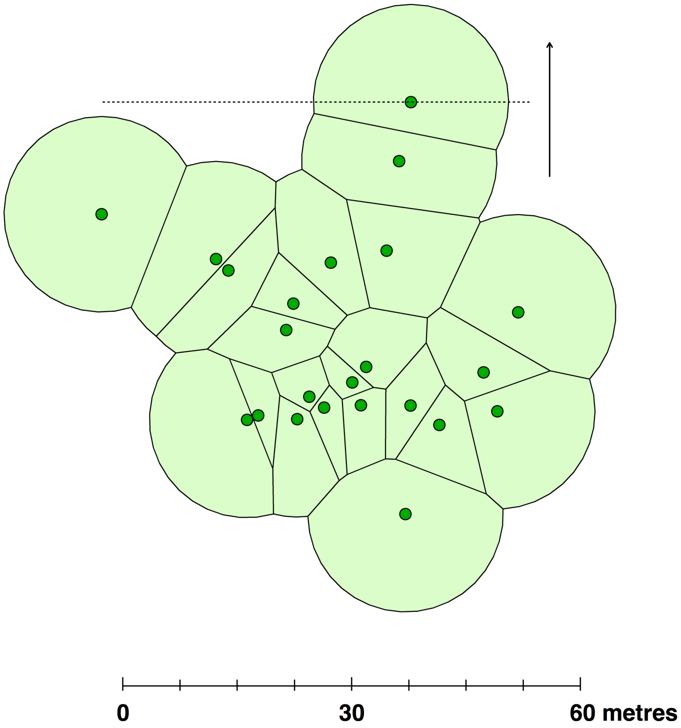

Figure 1. An example of the interpolated locations of troop members at a particular time (dark green circles), together with the estimated bounded domains of danger (light green areas) for each animal at that time. The direction of travel is indicated by the arrow. The dashed line, perpendicular to the direction of travel, drawn through the animal in the front of the group, provides the reference plane for the determination of each animal's distance from the front of the group.

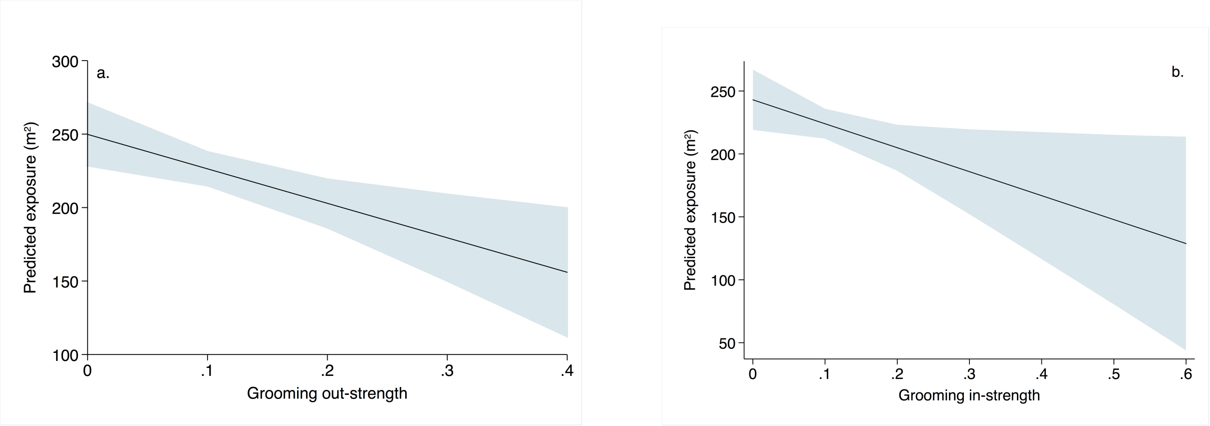

Figure 2. Predictive margins with 95% CIs for the relationship between exposure to risk and (a) grooming out-strength and (b) grooming in-strength for adult vervet monkeys.

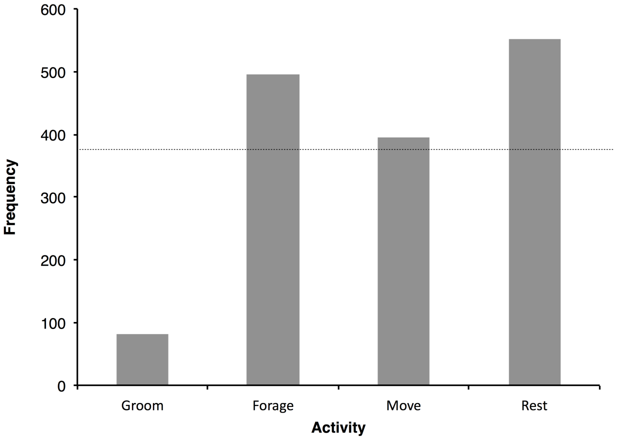

Figure 3. Activity at the times when animal spatial location was recorded. Activity budget estimates for all adult animals come from scan samples taken every 30 minutes. Data presented here come from scans of individual activity (N_{total}=1524. N_{groom}=81; N_{forage}=496; N_{move}=396; N_{rest}=551) recorded during the scan sample closest to the time at which each spatial sweep was conducted. Dashed line indicates frequencies expected from a uniform distribution.

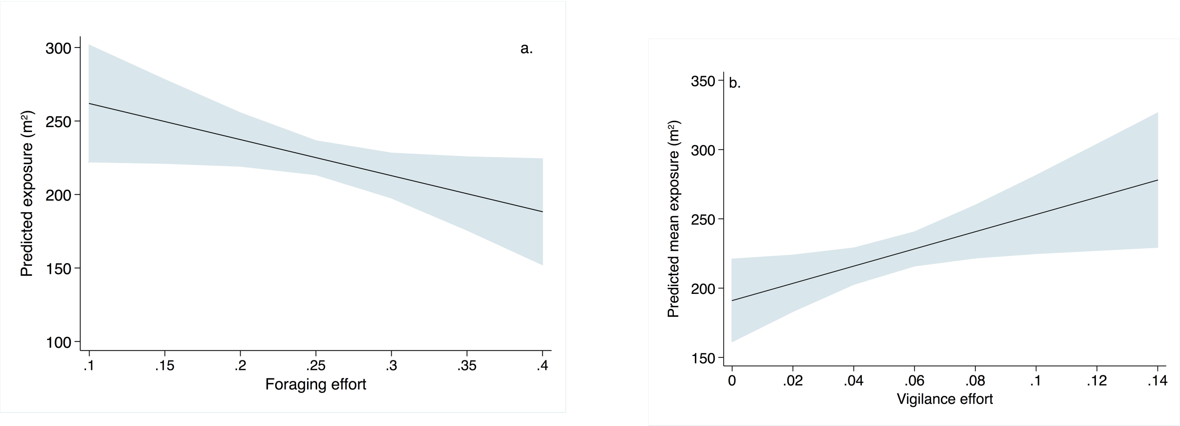

Figure 4. Predictive margins with 95% CIs for the relationship between mean exposure to risk and (a) foraging effort and (b) vigilance for adult vervet monkeys.

Table 1. Results from the linear mixed model analysis to test the fixed effects of dominance rank, grooming out-strength and grooming in-strength on exposure to risk and distance from the front of the troop. Animal sex and the troops to which they belonged were entered as control variables. Animal identity was entered as a random effect to control for repeated measures.

	β	SE	Z	P	95% CI	
a. Exposure to risk						
Sex (Ref: Female)	5.097	15.853	0.320	0.748	-25.974	36.167
Troop (Ref: PT)	-31.833	16.162	-1.970	0.049	-63.510	-0.157
Rank	-20.418	30.567	-0.670	0.504	-80.328	39.492
Grooming out-strength	-254.865	78.307	-3.250	0.001	-408.343	-101.387
Grooming in-strength	-141.073	71.987	-1.960	0.050	-282.165	0.018
Intercept	301.493	26.633	11.320	0.000	249.294	353.693
b. Distance from the front of the troop						
Sex (Ref: Female)	0.046	0.025	1.83	0.067	-0.003	0.095
Troop (Ref: PT)	-0.013	0.016	-0.82	0.411	-0.045	0.018
Rank	0.002	0.063	0.03	0.978	-0.121	0.124
Grooming out-strength	0	0.005	0.07	0.944	-0.01	0.011
Grooming in-strength	0.007	0.007	1.02	0.310	-0.007	0.021
Intercept	0.44	0.036	12.34	0.000	0.37	0.51

Table 2. Results from the linear model to test the consequences of (a) the extent of mean exposure to risk and (b) mean distance from the front of the group on vigilance and foraging effort. Animal sex and the troops to which they belonged were entered as control variables.

	β	**SE**	**t**	**P**	**95% CI**	
a. Exposure to risk						
Sex (Ref: Female)	18.941	13.996	1.35	0.184	-9.4187	47.301
Troop (Ref: PT)	-0.798	12.330	-0.06	0.949	-25.781	24.184
Vigilance	621.106	262.700	2.36	0.023	88.824	1153.389
Foraging	-245.331	118.344	-2.07	0.045	-485.119	-5.542
Intercept	244.509	36.702	6.66	0.0001	170.143	318.875
b. Distance from front						
Sex (Ref: Female)	0.046	0.020	2.32	0.026	0.005	0.087
Troop (Ref: PT)	-0.026	0.017	-1.48	0.146	-0.062	0.009
Vigilance	-0.382	0.379	-1.01	0.321	-1.151	0.386
Foraging	0.023	0.171	0.13	0.894	-0.323	0.369
Intercept	0.488	0.053	9.19	0.0001	0.381	0.595